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The effects of past, present and future climate change on range-wide genetic diversity in northern North Atlantic marine species

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Abstract:

It is now accepted that changes in the Earth's climate are having a profound effect on the distributions of a wide variety of species. One aspect of these changes that has only recently received any attention, however, is their potential effect on levels of within-species genetic diversity. Theoretical, empirical and modelling studies suggest that the impact of trailing-edge population extirpation on range-wide intraspecific diversity will be most pronounced in species that harbour the majority of their genetic variation at low latitudes as a result of changes during the Quaternary glaciations. In the present review, I describe the historical factors that have determined current patterns of genetic variation across the ranges of Northern North Atlantic species, highlight the fact that the majority of these species do indeed harbour a disproportionate level of genetic diversity in rear-edge populations, and outline how combined species distribution modelling and genetic analyses can provide insights into the potential effects of climate change on their overall genetic diversity.

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The effects of past, present and future climate change on range-wide genetic diversity in northern North Atlantic marine species

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Abstract. It is now accepted that changes in the Earth's climate are having a profound effect on the distributions of a wide variety of species. One aspect of these changes that has only recently received any attention, however, is their potential effect on levels of within-species genetic diversity. Theoretical, empirical and modelling studies suggest that the impact of trailing-edge population extirpation on range-wide intraspecific diversity will be most pronounced in species that harbour the majority of their genetic variation at low latitudes as a result of changes during the Quaternary glaciations. In the present review, I describe the historical factors that have determined current patterns of genetic variation across the ranges of Northern North Atlantic species, highlight the fact that the majority of these species do indeed harbour a disproportionate level of genetic diversity in rear-edge populations, and outline how combined species distribution modelling and genetic analyses can provide insights into the potential effects of climate change on their overall genetic diversity.

Keywords. Distribution range, extinction, extirpation, phylogeography, refugium, species distribution modelling

Introduction

Shifts in species' ranges in response to recent climate change have been observed across a wide range of taxa, including marine species (Parmesan and Yohe 2003, Perry et al. 2005, Hickling et al. 2006, Lima et al. 2007, Kelly and Goulden 2008). Climate-mediated changes in the distributions of organisms are not a new phenomenon, however: the ice ages of the Quaternary period (*ca.* 2.6 MA–present) resulted in periodic episodes of retreat into climatically suitable refugia for many species, followed by expansion during subsequent warming phases (Hewitt 1999, Provan and Bennett 2008). One consequence of these fluctuations is that genetic variation is often not distributed evenly across species' ranges, with former refugial areas instead harbouring a large proportion of the total diversity (Hampe and Petit 2005). Given that such rear edge populations are those most immediately under threat from climatic change, many researchers are now considering the possible effects of extirpation of rear-edge populations on the overall genetic diversity within a species (Beatty and Provan 2011, Bálint et al. 2012, Pro-

van and Maggs 2012). Loss of genetic diversity is considered extremely detrimental from a conservation point of view, since low levels of diversity are generally correlated with reduced adaptive potential (Allendorf and Luikart 2007). The aim of the current review is to describe the processes that have shaped the distribution of genetic variation across northern North Atlantic marine species ranges, and to highlight the potentially disproportionate impact of rear-edge population extirpation on intraspecific genetic diversity.

Previous climate change and species' ranges

Throughout the Quaternary period, the Earth's climate has fluctuated periodically as a result of changes in both its orbital distance from the sun and the obliquity of its spin, and from the precession of its rotational axis (Hays et al. 1976). These Milankovitch Cycles gave rise to the Ice Ages, long (*ca.* 100 KY) cold periods interspersed with short (*ca.* 10–15 KY) interglacial periods. During the glaciations, many northern hemisphere species, and particularly those adapted to temperate conditions, only persisted in climatically suitable refu-

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glacial areas, usually south of the ice sheets and permafrost (Hewitt 1999, Bennett and Provan 2008, Provan and Bennett 2008). In the case of marine species, and in particular for intertidal invertebrates and algae, which generally are not well-represented in the fossil record, most insights into their response to the glaciations have been gained from phylogeographic analyses (reviewed in Maggs et al. 2008). During the Last Glacial Maximum (LGM; *ca.* 21 KYA), the combination of reduced sea temperatures and a drop in sea level of up to 130 m drastically changed the distribution of many marine species, and genetic evidence has indicated several key refugial regions on both sides of the North Atlantic (summarised in Figure 1: for more detail see Maggs et al. 2008 and Table S5 in Provan and Maggs 2012). As well as identifying “classic” southern refugia in the Iberian peninsula and on North American coastlines south of the limit of the Laurentide Ice Sheet at the LGM, these phylogeographic studies have often also highlighted the existence of “cryptic” refugia on both sides of the North Atlantic, e.g., the “Hurd Deep” in the English Channel (Provan et al. 2005) and Atlantic Canada (Wares and Cunningham 2001). Furthermore, palaeodistribution modelling studies, which involve the hindcasting of species distributions based on LGM climate reconstructions, have confirmed several refugial areas for North Atlantic fish (Bigg et al. 2008), algae (Provan and Maggs 2012) and invertebrates (Provan et al. 2009, Waltari and Hickerson 2012) suggested by

phylogeographic analyses.

Genetic variation across species’ ranges

It is now becoming clear that the distribution of genetic variation across species’ ranges is the result of a combination of historical and contemporary factors. Previously, it had generally been assumed that levels and patterns of intraspecific genetic diversity reflected the “abundant-centre” model of species’ distributions, where higher population density in the centre of the range was reflected in highest levels of genetic diversity, with a decrease as one moves towards the edge of the range (Vucetich and Waite 2003, Eckert et al. 2008). Recently, though, it has been suggested that large-scale, historical forces have played a greater role in shaping the observed patterns of genetic diversity across species’ ranges, and that simple central-marginal models of range-wide genetic diversity are complicated by the signatures of glacial persistence and postglacial recolonization (Hampe and Petit 2005). Refugial areas are typically characterised by high levels of genetic variation, including the occurrence of private haplotypes i.e. those not found elsewhere in the species’ range, whilst recolonized areas show reduced genetic diversity and are generally comprised of a subset of genotypes from their source refugia (Taberlet et al. 1998, Provan and Bennett 2008). This historical diversity found in LGM refugia is the result of long-term persistence, often through several glacial maxima, and divergence, and can be

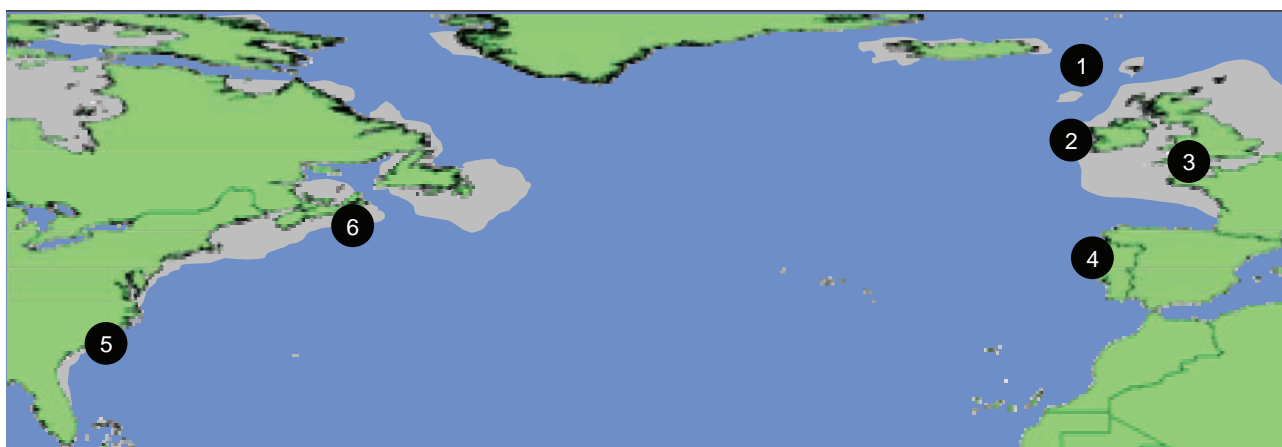


Figure 1. Locations of glacial refugia for northern North Atlantic species revealed by phylogeographic analyses. 1 – Faeroes / Southern Iceland (exact location unclear); 2 – Southwestern Ireland; 3 – English Channel (“Hurd Deep”); 4 – Northwestern Iberia; 5 – Northeastern USA; 6 – Maritime Canada. Dry land at the LGM is indicated in grey.

retained in rear-edge populations despite the increased effects of genetic drift and prevalence of vegetative reproduction characteristic of the fragmented, peripheral populations generally found at species' range margins (Eckert 2002, Beatty et al. 2008, Diekmann and Serrao 2012).

The genetic signatures of refugial persistence during the LGM and postglacial recolonization are evident for many Northern North Atlantic marine species (Maggs et al. 2008). Most phylogeographic studies have revealed the characteristic reduction in genetic diversity with increasing latitude, although a few studies have indicated an area of high diversity with some unique haplotypes off the western coast of Norway, which might be indicative of a cryptic northern refugium (Roman and Palumbi 2004, Provan and Maggs 2012). Generally, though, the major refugial areas lay at low latitudes and, consequently, many rear-edge populations of these species represent reservoirs of unique genetic variation, which is increasingly coming under threat from climate change (Summarised in Table 1).

Potential effects of future climate change on genetic diversity

The current period of global climate change has already resulted in observed distributional shifts across a broad range of taxa (Parmesan and Yohe 2003, Perry et al. 2005, Hickling et al. 2006, Lima et al. 2007, Kelly and Goulden 2008). Whilst poleward shifts result from leading-edge migration (Thomas 2010, Hill et al. 2011), rear-edge range shifts are generally characterized by population extirpation rather than habitat tracking (Parmesan et al. 1999, Thomas 2005, Aitken et al. 2008, Gibson et al. 2009). A recent study demonstrated

that whilst rear-edge range contractions in terrestrial animals tend to "lag" behind their thermal optima, their marine counterparts show more immediate responses to climate change at both their leading and trailing edge boundaries (Sunday et al. 2012). Although the magnitude of extinction attributable to climate change has been the subject of recent debate (He and Hubbell 2011, 2012, Thomas and Williamson 2012), it is clear that rear-edge populations are most immediately under threat of extirpation.

In species where rear-edge populations maintain high levels of genetic variation, loss of these populations will have a disproportionately pronounced impact on overall genetic diversity. This loss could be exacerbated in cases where one or more southern refugia have not contributed to postglacial recolonization and thus harbour genotypes found nowhere else throughout the species' range (e.g., Bilton et al. 1998, Petit et al. 2003). A recent model-testing-based phylogeographic study confirmed that this is the case for European populations of the red seaweed *Chondrus crispus* (Provan and Maggs 2012). Recolonization of Europe by *C. crispus* took place primarily from a refugium in the English Channel, with little or no contribution from a separate Iberian refugium and, consequently, these rear-edge populations contain endemic genetic variation that is under immediate threat from ongoing recorded climate-induced range shifts (Lima et al. 2007).

Although model-testing and/or statistical phylogeographic approaches were not employed in any of the other studies highlighted in Table 1, it seems likely that this type of differential recolonization where species have persisted in multiple southern refugia, as well as leading-edge recolonization

Species	Description	Refugial location(s)	Reference
<i>Celleporella hyalina</i>	Bryozoan	Northwestern Iberia	Gómez et al. (2007)
<i>Chondrus crispus</i>	Seaweed	Northwestern Iberia	Provan & Maggs (2012)
<i>Fucus ceranoides</i>	Seaweed	Northern Iberia	Neiva et al. (2012)
<i>Littorina saxatilis</i>	Periwinkle	Northwestern Iberia	Doellmann et al. (2011)
<i>Monocelis lineate</i>	Microturbellarian	Northwestern Iberia	Casu et al. (2011)
<i>Nassarius nitidus</i>	Gastropod	Mediterranean / Northern Iberia	Albaina et al. (2012)
<i>Neomysis integer</i>	Mysid	Portugal	Remerie et al. (2009)
<i>Palmaria palmata</i>	Seaweed	Portugal	Provan et al. (2005)
<i>Pomatoschistus minutus</i>	Fish	Northwestern Iberia	Larmuseau et al. (2009)

Table 1. Northern North Atlantic species harbouring unique genetic variation in rear-edge populations.

zation processes, explains the high levels of unique genetic variation observed in rear-edge populations of many North Atlantic intertidal species which are currently threatened by climate change. Isolation of intertidal organisms in Iberian refugia could have been due to the lack of rocky substrate in the Bay of Biscay (Lüning 1990), and the continued absence of suitable habitat also represents a barrier to habitat tracking in the face of current global warming. Of the studies listed in Table 1, this appears most pronounced in the bryozoan *Celleporella hyalina* (Gómez et al. 2007), the periwinkle *Littorina saxatilis* (Doellmann et al. 2011), the mysid *Neomysis integer* (Remerie et al. 2009) and the fish *Pomatoschistus minutus* (Larmuseau et al. 2009), where rear-edge populations from Iberia were comprised exclusively of endemic haplotypes.

Where postglacial recolonization has not involved a simple expansion from southern refugia, patterns of range-wide genetic variation may be more complex. Species that have also persisted in northern refugia, will usually exhibit a less disproportionate skew of genetic diversity towards the rear edge (Beatty and Provan 2011). Such species tend to be cold-tolerant, and it is interesting to consider that whilst they are more likely to suffer from warming temperatures with respect to range contraction, their maintenance of genetic diversity at higher latitudes means that the effects on range-wide levels of genetic variation should be less pronounced than in temperate species that harbour the highest levels of diversity at the rear edge. Among northern North Atlantic marine species, this is particularly evident in the seagrass *Zostera marina* (Olsen et al. 2004) and the brown seaweed *Fucus ceranoides* (Neiva et al. 2010). Both of these cold-tolerant taxa exhibit relatively high levels of genetic diversity at higher latitudes as a result of proposed admixture from multiple refugia (*Z. marina*) and introgression (*F. ceranoides*), further highlighting the complex processes that can shape the distribution of genetic diversity across a species' range. Likewise, there are terrestrial examples of longitudinal recolonization i.e. west-to-east or vice-versa (Beatty and Provan 2010), although such a sce-

nario has not yet been clearly identified for a marine species.

It has been suggested that during the LGM, the vast majority of intertidal species were extirpated from the shorelines of North America due to glacial advances and the lack of suitable substrate on coastlines south of the limits of the Laurentide ice sheets, and that their current pan-Atlantic distribution is a result of recolonization from Europe (Ingólfsson 1992). Although a matter of ongoing debate in both genetic and modelling circles (e.g., Ilves et al. 2010, Waltari and Hickerson 2012), the occurrence of unique North American genotypes in several phylogeographic studies suggests possible persistence *in situ* during the LGM for at least some taxa (Wares and Cunningham 2001, Hickerson and Cunningham 2006, Bigg et al. 2008, Provan and Maggs 2012). As a result of these inconsistencies, the effects of climate change on intraspecific diversity in species found on either side of the North Atlantic should probably be considered on a species-by-species basis, rather than assuming any general patterns.

Species distribution modelling based on projected future climate scenarios is widely used to assess the potential impact of climate change on the ranges of terrestrial species (reviewed in Thuiller et al. 2008). Although such studies are as yet not as common for marine taxa as for their terrestrial counterparts, projections of the future distributions of North Atlantic fish (Lenoir et al. 2011) and invertebrates (Reygondeau and Beaugrand 2010, Rombouts et al. 2012) have recently been reported. Predictive modelling approaches are now being extended to incorporate the potential effects of range shifts and loss on intraspecific genetic diversity (Beatty and Provan 2011, Habel et al. 2011, Alsos et al. 2012, Bálint et al. 2012, D'Amen et al. 2013), and have confirmed the disproportionate impact of rear-edge population extirpation on range-wide genetic diversity. Additionally, the advent of next-generation sequencing approaches to identify genome-wide patterns of selection in natural populations (see Box 1) will allow us to identify whether such genetic erosion could have a major impact on adaptive potential (Stapley et al. 2010).

Box 1: Adaptive genetic variation at range margins and the promise of next-generation sequencing

Whilst the majority of phylogeographic studies across species' ranges have been based on neutral genetic markers, primarily chloroplast or mitochondrial DNA, it has been argued that peripheral populations could conceivably harbour unique adaptive variation that could be important in the face of global climate change, particularly at species' rear edges (Hampe and Petit 2005). The significance of adaptive genetic variation at species' range margins has been extensively debated, and to date remains poorly understood (Bridle and Vines 2006, Kawecki 2008, Sexton et al. 2009). Theoretical studies have suggested that asymmetric gene flow from differently adapted populations nearer the centre of the range will "swamp" any potentially useful adaptive variation present in marginal populations, although it has also been suggested that this could enhance the potential for adaptation under certain circumstances (Kirkpatrick and Barton 1997, Holt and Gomulkiewicz 1997).

In recent years, "genome scanning" approaches have been used to identify loci that exhibit evidence of selection in natural populations (Storz 2005). The majority of these have used amplified fragment length polymorphisms (AFLPs) to identify a small percentage of usually several hundred loci that are putatively under selection, including a single study comparing potential adaptive variation in central and peripheral populations (Parisod and Joost 2010). The advent of next generation sequencing (NGS) promises to revolutionize such studies, with the potential to analyze hundreds of thousands of loci. Restriction-site-associated DNA (RAD) sequencing in particular allows the high-throughput analysis of thousands of single nucleotide polymorphisms (SNPs) in multiple individuals at relatively low cost (Baird et al. 2008, Davey et al. 2011). This approach has been used previously in stickleback populations to identify SNPs linked to loci involved in adaptation to freshwater habitats (Hohenloehe et al. 2010). The volume of sequence data generated in a single NGS run means that "genotyping by sequencing" approaches can be used to identify SNPs *de novo*, even in non-model organisms. Such studies will shed important light on the relative distribution of neutral and adaptive variation across species ranges and, given that intertidal organisms can occupy a wide range of micro-habitats, it is possible that important adaptive variation might also be found in non-marginal populations (Helmuth et al. 2003).

Conclusions and prospects

Previous debate about the conservation value of peripheral populations has now been put firmly into focus by the current and future impact of global climate change on species' distribution ranges, particularly at the rear edge (Lesica and Allendorf 1995, Hampe and Petit 2005, Gibson et al. 2009). Knowledge of how genetic diversity is distributed across species' ranges is intrinsic to the notion of which populations are valuable for conservation, and a growing body of research is attempting to combine modelling and genetic approaches to address this issue. Whilst such an approach has not as yet been applied to northern North Atlantic marine taxa, there have been great developments in each of the individual fields. The availability of future models of sea-surface temperature, salinity, etc., and the growing availability of genetic data (both existing and *de novo*) will

allow us to gain new insights into the effects of a changing world on northern North Atlantic marine ecosystems.

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